THE PERMIAN BRACHIOPOD GENUS HORRIDONIA CHAO

by D. J. GOBBETT

ABSTRACT. Horridonia is redefined to include two variable species, H. horrida and H. timanica. The lectotype of the former is redescribed and figured. H. timanica is a Russian and Arctic species, H. horrida European. Both species occur in Greenland. The genera Sowerbina Fredericks emend. Dunbar and Pleurohorridonia Dunbar are considered synonymous with Horridonia.

In the classification of the Productidae, the surface sculpture of the ventral valve has always played an important role (discussion in Chao 1927). However, Tschernyschew (1902) considered the form of both valves and the shell cavity, and Fredericks (1915) defined three groups on this basis which he called *Producti typici* α , *P. typici* β , and *P. proboscidei*. He criticized Thomas's (1914) classification and considered that the surface sculpture was an adaptive character, depending on the mode of life of the organism.

Chao (1927) recognized three principle factors: surface sculpture, the form of the valves and the shell cavity, and the internal characters. He defined *Horridonia* (p. 24) as: 'Characterised by strong median sinus and fold, slightly convex brachial valve and a few but very stout hollow spines. Type, *Productus horridus* Sowerby and *Productus timanicus* Stuckenberg.' The following year he expanded this slightly (Chao 1928, p. 62) as follows: 'Forms belonging to this sub-section, [*Horridonia*] . . . possess essentially the same characteristic outline of typical *Productus*, but are without either plicae or wrinkles. The median sinus and fold are rather pronounced and the surface is marked only by irregularly distributed, strong and erect spines. Some indefinite plicae are sometimes present, indicating occasional survival of the plica-making impulse.'

In 1928 Fredericks, presumably ignorant of Chao's work, produced a classification of the genus *Productus* based primarily on his three morphological groups and secondarily on the surface sculpture of the visceral part of the valves. He defined a genus *Sowerbina* in Russian (Fredericks 1928) with an English summary (p. 789) as follows: 'The shell is productiform and has a plain surface. Sometimes a thin granulation is observed on the surface of the valves. Sometimes are seen marks of a punctate structure. Type *Productus timanicus* Stuckenberg spec.'

Neither of these authors has given a satisfactory definition of a genus which includes *P. horridus* Sowerby and *P. timanicus* Stuckenberg. Chao's name, *Horridonia*, has priority. He designated two genosyntypes, *P. horridus* Sowerby and *P. timanicus* Stuckenberg, the first of which was selected as genolectotype by Schuchert and LeVene (1929). Later writers have enlarged the genus to include various forms having a smooth shell surface with scattered spines and often a ribbed trail. Branson (1948) lists thirteen species, some of which had been referred to *Avonia* by previous authors; some were put into new genera by Muir-Wood and Cooper (1960) and others are synonyms or inadequately described.

Pala centology, Vol. 4, Part 1, 1961, pp. 42-53, pls. 3-5.]

Dunbar (1955) has recognized the genus Sowerbina Fredericks as distinct from Horridonia Chao. Dunbar's diagnosis of Sowerbina (p. 96) is as follows: 'Productids of moderate to strong curvature (not geniculate), having a narrow ventral sulcus between strong visceral humps; cardinal extremities extended into conspicuous auricles; surface non-costellate, ornamented by minute crinkly pustules; spines large, specialized, and localized as follows: the dorsal valve bears a single row of cardinal spines plus a pair (rarely more or less) of large spines on each auricle, ventral valve without cardinal or auricular spines but having 1 to 3 (rarely more) radial rows of spines on the visceral humps. Generotype: Productus timanicus Stuckenberg.'

Sowerbina as defined by Dunbar differs essentially from Horridonia Chao in the absence of cardinal and auricular spines on the ventral valve. Except in this character, the extent and size of the spines in P. horridus and P. timanicus are extremely variable. It seems best at present to refer both species to Horridonia.

Genus HORRIDONIA Chao

1927 Horridonia Chao, p. 25.

1928 Sowerbina Fredericks, p. 778.

1955 Pleurohorridonia Dunbar, p. 89.

1955 Sowerbina Fredericks, Dunbar, p. 95.

Generic description. Productids, trapezoidal in outline, with auricles moderately to strongly developed. Ventral valve moderately to strongly convex, not geniculate; median sulcus deep to very shallow, dividing more or less prominent visceral humps. Dorsal valve almost flat to markedly concave, with median fold. Surface of both valves smooth or with a very fine granular sculpture; visceral surface of ventral valve usually with erect spines; anterior part of this valve often with irregular costae. Long cardinal and auricular spines present on both valves or dorsal valve only. Interior of ventral valve with a prominent adductor muscle platform. Interior of dorsal valve with median septum between triangular adductor muscle impressions. Cardinal process trilobed, the central lobe bifid, posterior surface of lobes pectinated.

Type species by subsequent selection of Schuchert and LeVene (1929, p. 68): Productus horridus J. Sowerby 1823.

Horridonia horrida (J. Sowerby)

Plate 3, figs. 1–12; Plate 5, figs. 5, 7–8

1823 Productus horridus J. Sowerby, p. 17, pl. 319, fig. 1.

1829 Producta calva J. de C. Sowerby, p. 115, pl. 560, figs. 2-6.

1846 *Productus geiuitzianus* de Koninck, p. 264, pl. 15, figs. 3 *a*–*d* (reprinted in de Koninck 1847, p. 156, pl. 15, figs. 3 *a*–*d*).

1848 Productus latirostratus Howse, p. 256.

1848 Productus umbonillatus King, p. 8.

1850 Productus horridus Sow.; King, p. 87, pl. 11, figs. 1–13.

1850 Productus umbouillatus King, p. 92, pl. 11, figs. 14–18.

1858 Productus sulcatus Sow, var. borealis Haughton, part, p. 242, pl. 7, figs. 1 and 7.

1861 Productus horridus Sow.; Geinitz, p. 103, pl. 19, figs. 11-17.

1861 Productus latirostratus Howse; Geinitz, p. 102, pl. 19, figs. 7–10.

1861 Productus geiuitzianus de Koninck; Geinitz, p. 105, pl. 19, figs. 18–21.

? 1908 Productus borealis Whitfield, part, not Haughton, p. 55, pl. 2, fig. 11.

1909 Productus horridus Sow.; Eisel, p. 33, figs. 1-10.

1933 Productus horridus Sow.; Frebold, pp. 18, 20, 21, pl. 2, figs. 10–13, pl. 3, figs. 9 a-d.

1937 Productus horridus Sow.; Malzahn, p. 8, pl. 1, figs. 1-23, pl. 2, figs. 1-20.

1955 Pleurohorridouia scoresbyensis, Dunbar, p. 90, pl. 11, figs. 1-10.

1959 Horridonia horrida (Sow.); Stepanov, p. 191, pl. 1, figs. 1-6.

Type specimeu. The specimen figured by J. Sowerby (1823, pl. 319, fig. 1), British Museum No. B60972, has been generally accepted as the type, e.g. King 1850, p. 89, footnote. It is here formally designated the lectotype.

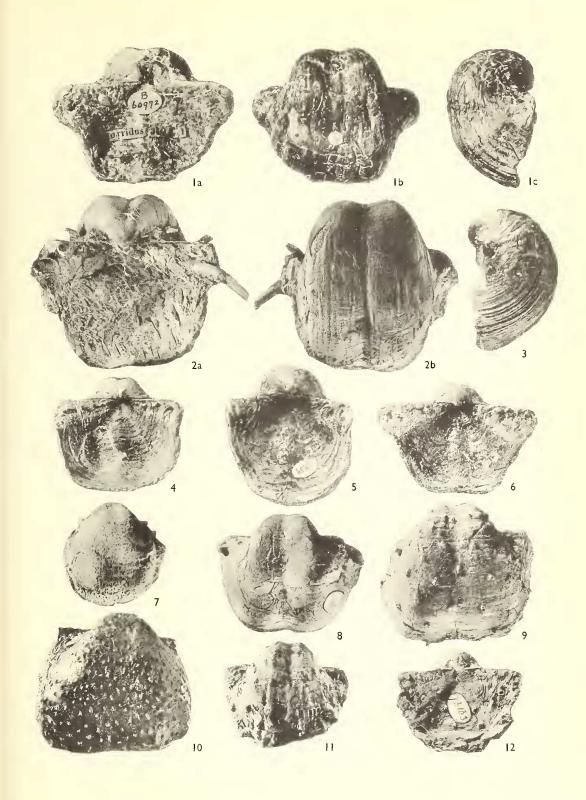
Type locality. The origin of the lectotype is obscure. Sowerby (1823, p. 17) records the locality as follows: 'Not very rare in Derbyshire, communicated by Mr. White Watson, from the seventh bed of his first Limestone, probably Magnesian, as it is above the coal series.' White Watson (1811, p. 5) describes the seventh bed of his first limestone, which forms the base of the Lower Magnesian Limestone, as follows: 'Shell-Limestone, of a more compact texture, of a bluish grey colour, containing petrified Bivalve Shells; this stone is in request for making Lime for Agriculture, and quarries of it are worked at Bolsover, Oxcroft, Barlborough, Palterton, and Houghton.' Gibson and Wedd (1913, p. 90) record disused quarries at Limekiln Field, north of Bolsover. This exposure is now much overgrown and on a recent visit no fossils were found. However, farther north at Aldfield, near Ripon, and at East Thickley in County Durham, H. horrida occurs in a hard, bluish limestone at about the same horizon as the limestone at Bolsover. The type locality of H. horrida may well be the disused quarry in Limekiln Field, Bolsover, Derbyshire (Grid. Ref. SK/474712). There is little doubt that the lectotype was collected from the Lower Magnesian Limestone.

Specific diagnosis. Horridonia with cardinal and auricular spines on both valves.

Description. The lectotype is figured on Plate 3, figs. 1a-c. It has a strongly convex auriculate ventral valve with a very broad sulcus and a double row of cardinal spines. On the anterior part of the ventral valve are irregular and rather coarse costae. The dorsal valve is moderately concave and has two rows of cardinal spines, the anterior row consisting of two or three spines only. The auricle is deflected to allow the passage of a large auricular spine. Sowerby's figure, although crude, is truer than King's (1850, pl. 11, fig. 2) which is an imagined restoration. In other specimens the sulcus may be narrower (Pl. 3, fig. 2b) or be almost absent (Pl. 3, fig. 7). The relative size of the auricles varies (Pl. 3, cf. figs. 4-6) and costae may be absent from the anterior part of the ventral valve. Only one row of cardinal spines may be present (Pl. 3, fig. 2a) and the auricular spine or spines are often small, though rarely absent. A variable number of visceral spines is present on the ventral valve (Pl. 3, cf. figs. 8-10), and occasionally on the dorsal valve (Pl. 3, fig. 12). In some specimens visceral spines are completely absent. The internal features are best studied on the internal moulds abundant in the Middle Magnesian Limestone at Humbledon Hill quarry, County Durham. Latex casts were made

EXPLANATION OF PLATE 3

Figs. 1–12. Horridonia horrida (J. Sowerby). Natural size. 1*a*–*c*, Dorsal, antero-ventral and lateral views of the holotype, B.M. B60972, figured by Sowerby 1823, pl. 319, fig. 1. Lower Magnesian Limestone, ? Bolsover, Derbyshire. 2*a*–*b*, Dorsal and ventral views, S.M. G823, Lower Magnesian Limestone, Harworth Main Sinking, Doncaster, Yorkshire. 3, Lateral view, B.M. B39307, Lower Zechstein, Trebnitz, Gera. 4, Dorsal view, B.M. B8727, Lower Zechstein, Gera. 5, Dorsal view, B.M. 65631, Budenguen. 6, Dorsal view, B.M. B39300, Posneck, Thuringia. 7, Ventral view, S.M. G1074, Lower Magnesian Limestone, Scar Lime Kilns, Well, Ripon, Yorkshire, G.R. SE/267813. 8, Ventral view, B.M. B5817, Lower Magnesian Limestone, East Thickley, Durham. 9, Ventral view, B.M. B39302, Lower Zechstein, Trebnitz, Gera. 10, Ventral view, B.M. 73248, same locality as fig. 9, 11–12, Ventral and dorsal view of two specimens, B.M. 73163, same locality as fig. 9.



GOBBETT, Horridonia horrida, \times 1



from these specimens (Pl. 5, figs. 5, 7–8). In the interior of the ventral valve, the umbone and hinge-line are quite smooth. The adductor muscle impressions lie on a raised platform which is parallel-sided, rounded anteriorly, and extends slightly anterior to the divaricator impressions. The latter are rounded-triangular in outline and are abruptly terminated anteriorly. The anterior and lateral parts of the valve are studded with small elongated pits. In the dorsal valve interior there is a smooth, flat area at the base of the cardinal process. The latter has three serrated lobes, the central one being bifid (Pl. 5, fig. 5). The adductor muscle impressions form a convoluted pattern and are triangular in outline. A median septum arises between these and runs anteriorly as far forward as the anterior border of the 'brachial impressions'. The latter are approximately oval with a raised rim. The posterior part of the valve is smooth or pitted. The anterior part has evenly spaced pustules, becoming larger and more densely spaced anteriorly.

Discussion. The representatives of this species show a great variation in external appearance. Forms from the English Zechstein were early recognized as distinct species, Productus horridus J. Sowerby, P. calvus J. de C. Sowerby, and P. latirostratus Howse = P. umbonillatus King. The last of these differs from other forms of H. horrida in its smaller size, low convexity of the ventral valve, and flattened umbo. It appears to be a stunted form, which perhaps lived in a less favourable environment. Eisel (1909) named and described six forms from the Zechstein of the Gera basin. He considered these to be varieties of P. horridus. The first of Eisel's varieties, var. initialis, was not found above bed 3, the 'Dachfloz' of the Gera Zechstein, but all the other varieties occurred together in bed 4, the 'Unterer Kompakter Zechstein'.

Malzahn (1937) gave a full discussion of *Productus horridus* and its varieties. He thought P. timanicus was a closely related ancestral species, connected with P. horridus by transitional forms. A specimen from central east Greenland described by Frebold (1933) as P. horridus Sow. var. granulifera Toula was cited as one of these transitional forms. Toula's variety is in fact Horridonia timanica (Stuck.). Frebold's specimen has cardinal spines on the ventral valve and belongs to H. horrida. Malzahn investigated the distribution of Eisel's varieties in new exposures of beds 3-5 in the Gera Zechstein. He confirmed that, although *initialis* was restricted to bed 3, any one of the other varieties was not restricted to any particular horizon within bed 4 and was thus of no stratigraphic use. In order to ascertain the relations between the varieties of P. horridus and P. timanicus, Malzahn selected three shell characters, the length of the hinge-line, the height of the ventral valve and the curvature of the ventral valve from umbo to anterior border. He subjected these to a statistical analysis and concluded that, with regard to these three characters, P. timanicus and four varieties of P. horridus form a genetically connected group. One variety, var. hoppeianus, does not fall into this group and on this statistical basis cannot be shown to be genetically related to it. However, if characters other than those selected for analysis are used, e.g. cardinal spines, hoppeianus would agree with the other varieties of P. horridus while P. timanicus would appear as the exception. A similar result would probably be obtained if internal characters were treated, e.g. the relative length of the septum in the dorsal valve.

Malzahn considered also the dependence of individual varieties on the type of sediment on which they lived. The shells in the Zechstein of Gera are commonly found with well preserved cardinal spines reaching a length of 10 cm., so that it may be assumed

that they constitute a biocoenose. They are restricted to a limestone or marly facies and are not found in the basal Zechstein conglomerate nor in the upper beds, which approach an evaporite facies. He concluded that the CaCO₃ content of the sediment may be directly related to the size but not the form of the shells. However, populations do not seem to be centred round one particular variety and may include several varieties with transitional forms (Eisel 1909; Malzahn 1937).

The two syntypes of *P. sulcatus* var. *borealis* Haughton, which were kindly lent to me from the National Museum of Ireland, represent two species. The larger specimen belongs here. It is well preserved and agrees precisely with a specimen in the Sedgwick Museum, G 832 (Pl. 3, fig. 2*a*–*b*), from the Lower Magnesian Limestone of Yorkshire. The smaller specimen, described by Haughton as a juvenile specimen, is generically distinct from *Horridonia*.

Some specimens from central east Greenland were described by Dunbar (1955) as a new species, *Pleurohorridonia scoresbyensis*. The diagnostic characters of this species, i.e. the ribbed anterior part of the ventral valve, the auricular spines, and the concentric granular surface sculpture, are all present on *Horridonia horrida*. Dunbar's form is perhaps nearest to Eisel's var. *hoppeianus*.

The great variation of *H. horrida* is illustrated in Plate 3. Varietal names are not recognized by the International Commission on Zoological Nomenclature and, although it may be convenient to describe the forms of *H. horrida* as subspecies, I think this is unwise. The variable characters, external form and spinosity, may be phenotypic. Also, intermediate forms occur and the 'varieties' do not appear to be of stratigraphical use.

Distribution (text-fig. 1). H. horrida is found in the English Zechstein from the Marl Slate to the middle part of the Middle Magnesian Limestone (Reef B of Trechmann 1925), after which it was presumably exterminated by an inimical environment. In Germany it occurs in the Kupferschiefer and Zechsteinkalk of the Lower Zechstein. Again it seems that an inimical environment set in after these beds had been deposited. In central east Greenland this species appears common and widespread. Dunbar records it from the Schucherts Flod area in southern Scoresby Land, Clavering Ø, Nathorsts Fjord area, and at many other places. It is also found in blocks of Permian limestone in Triassic conglomerate of the Kap Stosch area. Haughton's specimen came from Hillock Point, Melville Island; Whitfield's was collected from Cape Sheridan, at 82° 27' N. in Ellesmere Island. Recently Stepanov (1959) has described a Zechstein brachiopod fauna including H. horrida from two bore-holes in southern Lithuania. H. horrida is unknown in arctic Europe and Russia.

Horridonia timanica (Stuckenberg)

Plate 4, figs. 1-4; Plate 5, figs. 1-4, 6, 9-13

1875 Productus timanicus Stuckenberg, p. 86, pl. 1, figs. 1-7.

1875 Productus horridus Sow. var. granuliferus Toula, p. 232, pl. 6, figs. 3 a-c.

1902 Productus timauicus Stuck., Tschernyschew, p. 638, pl. 30, fig. 5; pl. 57, figs. 1-6; text-figs. 78, 79.

?1908 Productus borealis Whitfield, part, not Haughton, p. 55, pl. 1, fig. 1.

1914 Productus tinuauicus Stuck.; Wiman, p. 75, pl. 17, figs. 19–21, pl. 18, figs. 1–6.

1914 Productus inflatus Wiman, part, not McChesney, pl. 14, fig. 1, pl. 15, figs. 3, 5.

1934 Ruthenia granulifera (Toula); Fredericks, p. 39, pl. 3, figs. 1–8, pl. 4, figs. 1–3.

- 1937 Productus (Horridonia) borealis Stepanov, not Haughton, p. 115, 175, pl. 4, figs. 1–3, pl. 5, figs. 1–4.
- 1937 Productus (Horridonia) timanicus Stuck.; Frebold, p. 21, pl. 4, fig. 4, pl. 7, figs. 2–3.
- ?1939 *Productus (Horridonia) borealis* Licharew and Einor, not Haughton, p. 55, 206, pl. 10, figs. 6–11, pl. 11, figs. 1–5.
- 1955 Sowerbina maynci Dunbar, p. 97, pl. 13, figs. 1–9.
- 1955 Sowerbina rudis Dunbar, p. 101, pl. 14, figs. 1–7, pl. 15, figs. 1–6.

Type specimen. Stuckenberg (1875) mentioned no holotype. I designate as lectotype the specimen figured by Stuckenberg (1875, pl. 1, figs. 3 a-c).

Type locality. The specimens described by Stuckenberg were collected from the River Indiga section of the Timan 'mountain limestone' (67° 30′ N. 49° E.).

Specific diagnosis. Horridonia with cardinal and auricular spines on the dorsal valve only.

Description. This is based mainly on eighty specimens from Spitsbergen, now in the Sedgwick Museum, Cambridge.

The shell is auriculate with a trapezoidal to pentagonal outline. It is generally larger than *H. horrida* and the valves are thicker. The ventral valve is gently to very strongly convex but rarely geniculate. A median sulcus separates well defined visceral humps, and irregular costae are often present on the anterior part. The visceral disk of the dorsal valve is flat with a median fold and is more rectangular in outline than the dorsal valve of *H. horrida*. The surface of both valves has a fine granular sculpture, often obscured by loss of the outer shell layer or by silicification. Spines on the ventral valve are limited to the visceral humps where they occur in one to three or more longitudinal rows. Cardinal and auricular spines are present on the dorsal valve; they vary in number and thickness.

The interior of the valve is similar to that of *H. horrida* but the divaricator muscle impressions are relatively larger and extend anterior to the adductor muscle platform. The interior of the dorsal valve has a median septum extending anterior to the brachial impressions and often reaching the anterior border. In Spitsbergen specimens the posterior half of the dorsal valve is raised and separated from the anterior half by a prominent step. The anterior border is often thickened and bears coarse pustules which may be sharply pointed. The cardinal process is similar in form to that of *H. horrida* but is relatively larger.

Variation. Apart from a single Russian specimen, the only specimens I have seen are from Spitsbergen. These show variation in convexity of the ventral valve, development of the auricles, and number of auricular spines on the dorsal valve. However, these forms occur together at the same horizon. The variation in this species has been noticed by Fredericks (1934) and Stepanov (1936; 1937), both of whom described their specimens as specifically distinct from H. timanica Stuck. Fredericks thought (presumably) that the granular sculpture formed the bases of fine spines lying tangential to the surface. He put the species into Ruthenia (= Waagenoconcha). His three subspecies, R. granulifera typica, R. granulifera gibbosa, and R. granulifera spitzbergensis, parallel Stepanov's Horridonia borealis granulifera, H. borealis borealis, and H. borealis granulifera ab.

auriculata respectively. Stepanov distinguishes between the two subspecies of borealis as follows:

borealis

Ratio of curvature of ventral valve to length of dorsal valve not exceeding 3.

Auricles strongly arched.

Dorsal valve considerably concave.

Anterior part of ventral valve distinctly costate.

granulifera
This ratio not exceeding 2.

Auricles not strongly arched.

Dorsal valve less concave.

Anterior part of ventral valve non-costate.

Stepanov's subspecies are also more or less equivalent to Dunbar's *rudis* (= *borealis*) and *maynci* (= *granulifera*).

In the Spitsbergen specimens I have studied, all these forms are represented and are connected by transitional types.

Discussion. Toula described this species in 1875 as Productus horridus var. granuliferus. I have been unable to discover whether he has priority over Stuckenberg 1875. The publishers of Toula's paper have no record of the date of its publication and I have been unsuccessful in tracing the date of publication of Stuckenberg's work. However, Stuckenberg's description and figures are more adequate than those of Toula and it seems justifiable to use Stuckenberg's name. His description is fairly complete but he strongly suggests that cardinal spines are present on the ventral valve and his figures show spine bases in this region (Pl. 5, fig. 10). The only Russian specimen I have seen was kindly lent to me by Professor Dunbar. It was collected by W. Kulien from the river Adz'va, 59° E., 67° N., and identified by Fredericks. This specimen is figured on Pl. 4, fig. 4a-c; there is no trace of cardinal spines on the ventral valve. However, in this specimen and also in specimens from Spitsbergen, opposite each dorsal cardinal spine there is a depression in the rather thin cardinal border of the ventral valve, and between

EXPLANATION OF PLATE 4

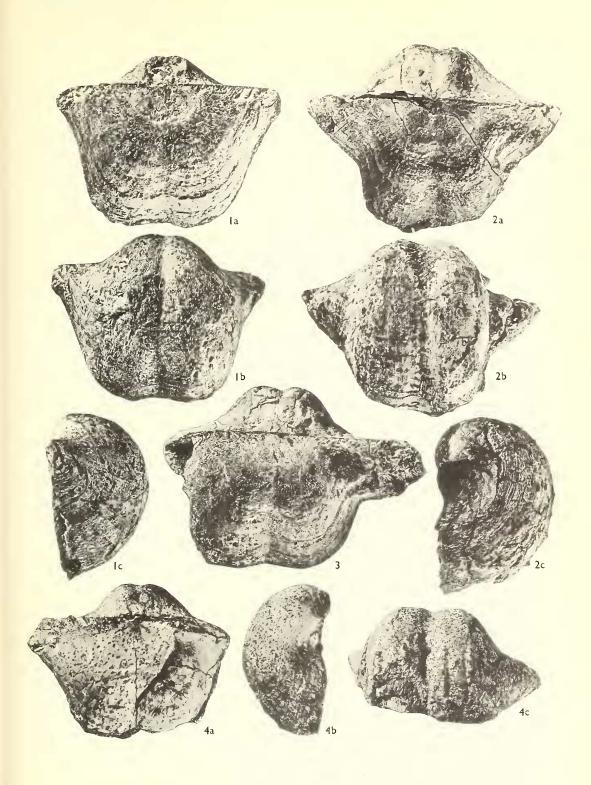
Figs. 1–4. *Horridonia timanica* (Stuckenberg). Natural size. 1*a*–*c*, Dorsal, ventral and lateral views, S.M. E17817, Limestone A (Spirifer Limestone), Templet, Bunsowland, Spitsbergen. 2*a*–*c*, Dorsal, ventral and lateral views, S.M. E17832, same locality as fig. 1. 3, Dorsal view, S.M. E17833, same locality as fig. 1. 4*a*–*c*, Dorsal lateral and anterior views, P.M. S2231, River Adz'va, Bolshezemelskaya Tundra, U.S.S.R., 59° E, 67° N.

EXPLANATION OF PLATE 5

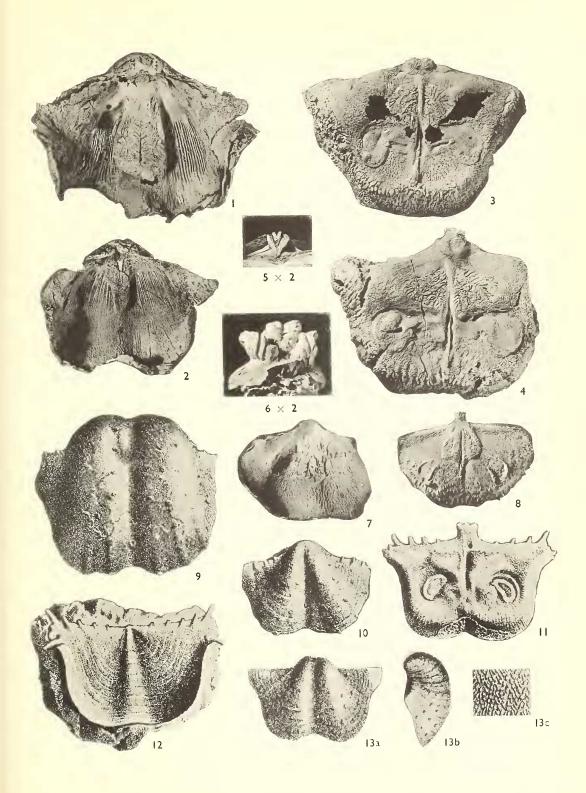
Figs. 1–4. Horridonia timanica (Stuckenberg). Natural size. Silicified valves treated with dilute HCl. 1, Ventral valve interior, S.M. E17822, Mertonberget, Ny Friesland, Spitsbergen. 2, Ventral valve interior, S.M. E17517, Limestone A (Spirifer Limestone), Gipshuken, Bunsowland, Spitsbergen. 3, Dorsal valve interior, S.M. E17608a, Limestone A (Spirifer Limestone), Tyrellfjellet, Bunsowland, Spitsbergen. 4, Dorsal valve interior, S.M. E17821, same locality as fig. 1.

Figs. 5, 7, 8. *Horridonia horrida* (J. Sowerby). Latex casts from natural internal moulds, Middle Magnesian Limestone, Humbledon Hill Quarry, Sunderland. 5, Reverse view of cardinal process, ×2, B.M. 43384. 7, Ventral valve interior, ×1, B.M. 97553. 8, Dorsal valve interior, ×1, B.M. 43384.

Figs. 6, 9–13. Horridonia timanica (Stuckenberg). 6, Reverse view of silicified cardinal process, ×2, S.M. E17823, Mertonberget, Ny Friesland, Spitsbergen. 9–12, Reproduction of original figures of *Productus timanicus* Stuckenberg 1875, pl. 1. figs. 1, 4, 2 a, 2 c, 9, Ventral valve anterior. 10, Ventral valve suggesting presence of cardinal spines (see discussion in text). 11, Dorsal valve interior. 12, Dorsal valve exterior. 13 a–c, Reproduction of original figures of *Productus horridus* Sow. var. granuliferus Toula 1875, pl. 6, figs. 3 a–c. a, Ventral view. b, Lateral view. c, Part of the shell surface, magnified.







GOBBETT, Horridonia